

Growth of *Dactylis glomerata* along a light gradient in the central Appalachian region of the eastern USA: II. Mechanisms of leaf dry matter production[☆]

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Received 30 October 2003; accepted in revised form 2 November 2004

Key words: Photosynthetic nitrogen use efficiency, Relative regrowth rate, Specific leaf area, Total non-structural carbohydrates

Abstract

Microsite influences development and resource allocation of *Dactylis glomerata* L. (orchardgrass), a traditional pasture species with potential as an understory crop in silvopasture of humid temperate regions. An experiment using container-grown orchardgrass was conducted under field conditions to determine how open (O), shaded woodland (W) and open-to-shaded woodland transition zone (E_O , E_W) microsites influenced leaf DM production. Plants established in spring (SP) and late summer (LS) were clipped each time mean canopy height reached 20 cm. Dry matter production and allocation among structures differed, as a function of light attenuation. Specific leaf area (SLA) and photosynthetic nitrogen-use efficiency (PNUE) were associated with leaf DM production, whereas leaf N, net assimilation rate and shoot total nonstructural carbohydrates (TNC), were not. Specific leaf area was related to leaf DM of LS plants, whereas PNUE influenced leaf DM of SP plants. Stembase TNC was inversely related to relative regrowth rate (RG_{RR}) with RG_{RR} greatest and TNC the least at W. The relationship for RG_{RR} and TNC for SP plants growing at O and LS plants growing at W was similar. Regardless of how indices of growth are related, SP and LS plantings responded as separate populations (representing young and established plants respectively) that have different leaf DM production efficiencies. Orchardgrass was able to sustain leaf production when subjected to simultaneous stresses of shade and repeated defoliation. The LS plants growing at W respond in a manner similar to SP plants and may require management practices attuned to establishing or immature plants.

Introduction

Silvopastoral systems, or systems that integrate forage production on a portion of the landscape occupied by trees, are complex and require management practices that function on different temporal and spatial scales simultaneously. Part of the complexity is caused by differences in resource

availability and allocation associated with microsite conditions. Agriculturalists consider these factors in terms of economically sound and environmentally benign means of generating a product or harvest index of a crop and not necessarily the mechanisms of how this is achieved by the plant. Ecologists, on the other hand, are interested in resource acquisition and allocation and quite often mechanisms thereof, as ways to predict system function and response to change on various temporal and spatial scales.

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Theories on how plants respond to resource availability and distribution differ. In some models, plants respond to resource supply by favoring structures and functions that enhance capture of the limiting resource(s). For example, increased allocation of dry matter to leaves or carbon assimilation mechanisms would occur if light were insufficient. Allometric theory proposes that dry matter is partitioned in ways corresponding to plant size because structures, and consequently functions, differ with size (Schwinning and Weiner 1998). Allocation ultimately influences competitive ability and thus productivity and persistence, with growth rate an important indicator of competitiveness (Van Andel and Biere 1990). McConnaughey and Coleman (1999) point out that many studies of resource allocation and underlying mechanisms of resource acquisition and allocation ignore morphological and physiological changes that occur as a matter of course in plant growth and development. They also note that the preponderance of work deals with undisturbed plant canopies grown for short periods with very young or very small plants. Models of how defoliated cool-temperate forage plants allocate resources in shaded environments are scarce (Kephart et al. 1992; Mosquera-Losada et al. 2001).

Devkota and Kemp (1999) reviewed the many aspects of temperate silvopastoral systems and concluded that successful and productive silvopastoral systems were based on shade-tolerant forages such as orchardgrass (*Dactylis glomerata* L.) that also tolerate repeated defoliation. Orchardgrass clipped frequently produced more herbage in shade than in open, whereas plants clipped infrequently were more productive in the open than in shade (Belesky and Mathias, unpublished data). Photosynthate allocation in orchardgrass depended on light environment and whether young or mature plants were defoliated (Belesky 2005a).

Understanding morphological and physiological processes that drive growth rates might help predict or identify management practices that optimize forage productivity in silvopastoral systems. The objective was to determine how conditions occurring in open pasture, shaded woodland and pasture-woodland transition zones that emulate well managed silvopasture sites, influence growth rate and components of

orchardgrass growth. Defoliation was based on mean sward surface height criteria for traditional open pasture applications.

Materials and methods

Experiment details are presented in Belesky (2005a). Briefly, grazing tolerant orchardgrass, cv. Benchmark, (early flowering) was sown (100 seed pot^{-1}) in 2.5 L pots containing a mixture of four parts soil (Lily, fine-loamy, siliceous, semi-active, mesic, Typic Hapludult) and three parts sand. Container-grown plants (with the pot bottoms removed) were used to eliminate or minimize site and soil related effects on germination, growth and nutrient availability. [Monaco and Briske (2000) present rationale for using container-grown plants.] Lime and fertilizer application was based on soil test results.

Prior to each experiment, plants were grown for six weeks in a growth chamber, with a 12 h photoperiod, 24/18 °C light/dark temperature and 55% relative humidity. Plants were placed outside the glasshouse in a non-shaded area for two weeks prior to placement at microsites in early May (spring planting, SP) or mid August (late summer planting, LS) of 2001. Microsites (81°7' W; 37°45' N; 850 m elev.) were within 60 m of each other and included an open (O) unobstructed pasture, a wooded (W) site dominated by mature *Quercus* spp. with approximately 89.8% light attenuation relative to O, and two edge (E) transition zones E_O and E_W (edge sites were south-facing exposures) with 30 and 56.4% light attenuation from similar tree species in W, respectively.

Sample collection and analysis

Baseline data were collected from nine pots for SP and LS immediately prior to planting. All plants were clipped to a 5-cm residual plant height. Plants from three replicates were harvested during the growing season each time mean extended leaf height reached 20 cm, with plant height, tiller number, leaf mass above 5 cm, stembase mass, (soil surface to 5 cm) and root mass determined. Tissues were freeze-dried and dry mass determined. Plants (grasses and forbs) surrounding the orchardgrass plants at each microsite were clipped to 5 cm height along with the experimental plants.

The SP plants were harvested in the year in which they were planted and the LS plants in the growing season after the year in which they were planted.

Total non-structural carbohydrates were determined for all components of harvested materials by an automated autoanalyzer hydrolysis method (Denison et al. 1990). Nitrogen was determined by combustion of dry plant tissue using a Carlo Erba EA 1108 CHNSO analyzer (Fisons Instruments, Beverly, MA, USA). Nitrates were determined by ion-selective electrode (Consalter et al. 1992).

Growth parameters

All values are expressed on a per tiller basis, normalized for 15 cm of top growth and five leaves per tiller. Tiller data are presented in Belesky (2000). The parameters of leaf area (A_L) related to the fresh mass of leaf (MF_L^{-1}), dry matter content of the leaf (DMC_L) and RGR calculated according to Ryser and Lambers (1995), photosynthetic nitrogen use efficiency (PNUE) according to Aerts (1990) and other parameters are computed according to Lambers et al. (1990) and Poorter (1990).

$$\begin{aligned} \text{Relative Regrowth Rate, } RG_RR \text{ (g g}^{-1}\text{d}^{-1}) \\ = (\text{NAR} * \text{LWR} * (1/\text{DMC}_L) * A_L/MF_L) \end{aligned} \quad (1)$$

$$\begin{aligned} \text{Net Assimilation Rate, NAR (g cm}^{-2}\text{d}^{-1}) \\ = ((1/\text{leaf area}) \\ (\text{DM}_{\text{top}} + \text{DM}_{\text{res}} + \text{DM}_{\text{root}})/(\text{T}_{2,3,4,5} - \text{T}_{1,2,3,4})) \end{aligned} \quad (2)$$

$$\begin{aligned} \text{Leaf Weight Ratio, LWR (g g}^{-1}) \\ = (\text{DM}_{\text{top}}/(\text{DM}_{\text{top}} + \text{DM}_{\text{res}} + \text{DM}_{\text{root}})) \end{aligned} \quad (3)$$

$$\begin{aligned} \text{DM Content of Leaf, } DMC_L \text{ (g g}^{-1}) \\ = (\text{DM}_{\text{top}}/(\text{fresh mass}_{\text{top}}/\text{tiller number})) \end{aligned} \quad (4)$$

$$\begin{aligned} \text{Specific Leaf Area, SLA (cm}^2\text{ g}^{-1}) \\ = (\text{leaf area per tiller}/\text{DM}_{\text{top}}) \end{aligned} \quad (5)$$

$$\begin{aligned} \text{Leaf Area per Mass Fresh Leaf,} \\ A_L/MF_L \text{ (cm}^2\text{ g}^{-1}) \\ = (\text{leaf area per tiller}/(\text{total fresh mass}_{\text{top}}/ \\ \text{tiller number})) \end{aligned} \quad (6)$$

Plant Nitrogen Use Efficiency, PNUE

$$\begin{aligned} (\text{g DM mol leaf N}^{-1}\text{d}^{-1}) \\ = (\text{g whole plant DM/mol leaf N}/\text{T}_{2,3,4,5} - \text{T}_{1,2,3,4}) \end{aligned} \quad (7)$$

Statistical analysis

Data were analyzed using SAS MIXED procedure. Light attenuation (sites O, E_O , E_W or W), harvest and planting time were fixed effects and replication was random in the model. Years were analyzed separately χ^2 test for homogeneity of variance failed; $p = 0.05$) in the model for light and harvest. Leaf DM was analyzed by SAS MIXED using the PDIFF option. There were apparent linear dependencies among parameters representing physiology and management (harvest, leaf N, RG_RR , SLA shoot TNC, NAR and PNUE). Therefore, total leaf DM production was tested for multi-collinearity between SP and LS plantings and by site, using the COLLININT option for multiple linear regression models. Leaf N, RG_RR , NAR and shoot TNC were omitted from the regression model based on the collinearity diagnostics, while harvest, SLA and PNUE were retained in the model.

Results and discussion

Available herbage (Leaf DM)

Dry matter production and allocation among parts of defoliated orchardgrass exposed to simultaneous stresses associated with light availability and defoliation depended on whether plants were juvenile or well-established (Belesky 2000). Cumulative leaf DM of SP plants differed ($p > F$, 0.001) among microsites, with 69% more leaf DM at O than W for five harvests made at each site (data not shown). Total leaf DM of LS plants did not differ among sites ($p_{0.05} > F$, = 0.26), with five harvests at W producing about 10% more DM than three harvests at O. The proportion of leaf relative to total plant DM did not vary as a function of light (Belesky 2000), but stembase DM (representing physiological response) and leaf morphology did. Mechanistic component analysis offers some insight into physiological and morphological responses of the plant to management

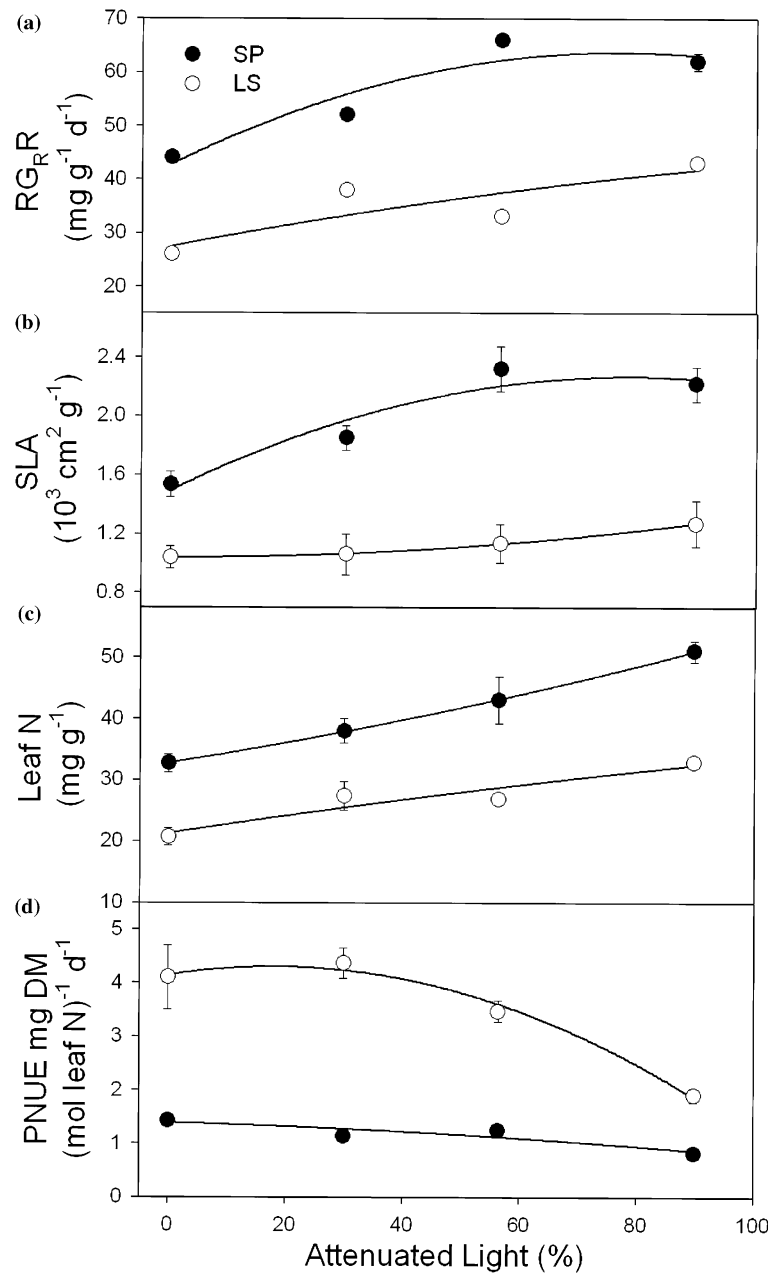


Figure 1. (a) Relative regrowth rate (RG_R); (b) specific leaf area (SLA); (c) leaf nitrogen (N); and (d) photosynthetic N-use efficiency (PNUE) expressed as a function of light attenuation for plants established in spring (SP) and late-summer (LS) in the central Appalachian Region of the eastern USA. Regression equations: $RG_{RSP} = 5.25(x) - 3.33 \times 10^{-3}(x^2) + 42.82$, $r^2 = 0.90$; $RG_{RLS} = 2.03 \times 10^{-1}(x) - 5.55 \times 10^{-4}(x^2) + 27.60$, $r^2 = 0.68$. $SLA_{SP} = 19.67(x) - 1.25 \times 10^{-1}(x^2) + 1494$, $r^2 = 0.92$; $SLA_{LS} = -4.57 \times 10^{-5}(x) + 2.89 \times 10^{-2}(x^2) + 1036.8$, $r^2 = 0.99$. $N: Y_{SP} = 1.53 \times 10^{-1}(x) + 5.51 \times 10^{-4}(x^2) + 32.75$, $r^2 = 0.99$; $N_{LS} = 1.46 \times 10^{-1}(x) - 2.54 \times 10^{-4}(x^2) + 21.30$, $r^2 = 0.89$. $PNUE_{SP} = -2.89 \times 10^{-3}(x) - 3.35 \times 10^{-5}(x^2) + 1.39$, $r^2 = 0.80$; $PNUE_{LS} = 1.71 \times 10^{-2}(x) - 4.73 \times 10^{-4}(x^2) + 4.14$, $r^2 = 0.99$.

and resource distribution, and may provide clues about how to optimize or sustain production. Defoliating canopies based on development

integrates morphological and phenological attributes of a forage plant with management and environment, and generally optimizes leaf

production, which sustains herbage productivity (Parsons et al. 1988) and nutritive value. Leaf production depends on the genetic potential of the plant, resource availability and management, especially in terms of regrowth occurring from one defoliation event to the next.

Relative regrowth rate (RG_{RR})

Relative regrowth rate (RG_{RR}) of leaves of SP and LS plants increased as the amount of light reaching the canopy surface decreased (Figure 1a). The greater RG_{RR} of SP than LS plants (Figure 1a) could be a product of larger LS plants (Belesky 2000) with resultant size related effects on growth rate. Genetic potential of the plant, temperature and water availability influence leaf extension and influence RG_{RR} . Defoliation based on a predetermined mean canopy height could increase RG_{RR} , since self-shading and the relatively slow growth of larger plants could be avoided, as would slow growth rates of plants clipped too soon after a previous defoliation event. The greater RG_{RR} of plants growing at W compared to the other sites reflects rapid leaf elongation that helps increase light capture and avoid shade.

Relative regrowth rate declined as total (leaf, stembase and root) DM increased (Figure 2). Where mass of SP and LS plants was similar ($< 100 \text{ mg tiller}^{-1}$), RG_{RR} was slightly greater for

LS than SP plants; however, RG_{RR} of the larger LS plants varied less where total DM exceeded $100 \text{ mg tiller}^{-1}$ (Figure 2).

Specific leaf area

Specific leaf area of SP and LS plants increased with increasing light attenuation (Figure 1b) with a 22% SLA increase in LS plants and a 44% increase for SP plants when comparing O to W. The difference could be that young or relatively small plants (characteristic of SP) adjust leaf morphology, whereas older or larger plants (LS) have means other than leaf morphology to avoid or tolerate shade and defoliation. Nonstructural carbohydrates in the stembase also sustain metabolic function and contribute to leaf elongation (Schnyder and Nelson 1987), and could enable plants to satisfy canopy development-based management criteria. Leaf DM tended to increase with stembase TNC concentration for SP and LS plants (Figure 3a). Plants grown at W had the least and at O the most leaf DM and stembase TNC relative to the other microsites, regardless of planting times. Leaf morphology can change when light is inadequate. Nonstructural carbohydrates appeared to have little relationship to SLA in LS plants, while a decline in SLA occurred as TNC increased in SP plants (Figure 3b). Shoot (leaf + stembase) TNC was greater in LS than SP plants, reinforcing observations that SP plants vary physiologically, whereas LS plants represent well established plants that are less likely to fluctuate metabolically in response to management and localized environment.

Leaf nitrogen

Classical RG_{RR} computations include a net assimilation (NAR) component that reflects the photosynthetic capability of the plant balanced with respiration. Thus, some understanding of DM production expressed as a function of N is warranted because of the strong relationship between tissue N and photosynthetic apparatus of C_3 grasses. Leaf N concentration increased as light attenuation increased (Figure 1c) and did so irrespective of plant part (data not shown). Hirose (1988) noted that relative growth rate and plant N

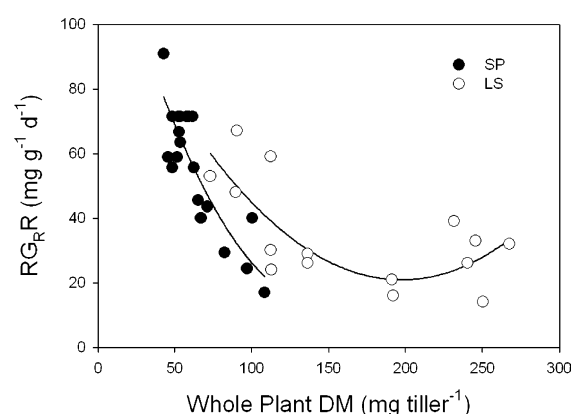


Figure 2. Relative regrowth rate (RG_{RR}) expressed as a function of whole plant DM for plants established in spring (SP) and late-summer (LS) in the central Appalachian Region of the eastern USA. Regression equations: $RG_{RR_{SP}} = -1.75(x) + 5.97 \times 10^{-3}(x^2) + 141.5$, $r^2 = 0.74$; $RG_{RR_{LS}} = -1.00(x) + 2.53 \times 10^{-3}(x^2) + 119.5$, $r^2 = 0.55$.

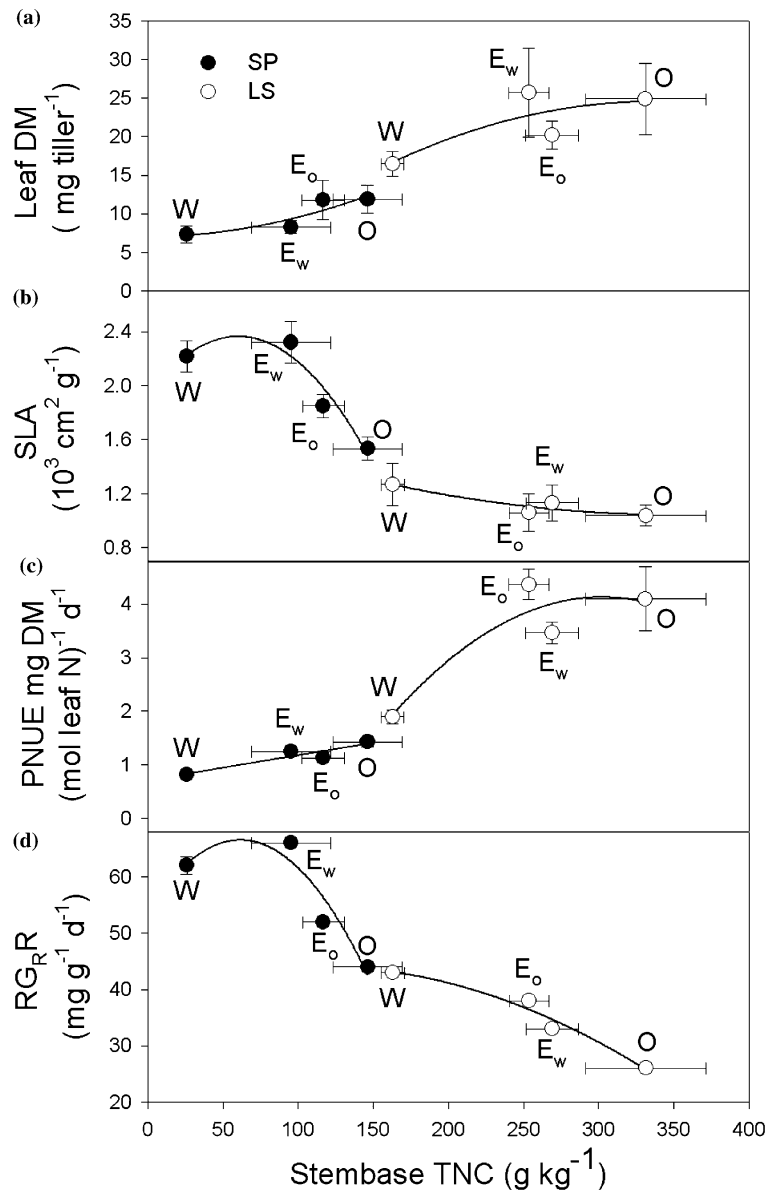


Figure 3. (a) Leaf dry matter (DM); (b) specific leaf area (SLA); (c) photosynthetic N-use efficiency (PNUE); and (d) relative regrowth rate (RG_R) expressed as a function of stembase total nonstructural carbohydrate (TNC) for plants established in spring (SP) and late-summer (LS) in the central Appalachian Region of the eastern USA. Regression equations: $DM_{SP} = 2.50 \times 10^{-3} (x) + 2.33 \times 10^{-4} (x^2) + 6.97$, $r^2 = 0.82$; $DM_{LS} = 1.76 \times 10^{-1} (x) - 2.62 \times 10^{-4} (x^2) - 4.98$, $r^2 = 0.66$. $SLA_{SP} = 14.12 (x) - 1.18 \times 10^{-1} (x^2) + 1938.7$, $r^2 = 0.92$; $SLA_{LS} = -4.36 (x) + 6.16 \times 10^{-3} (x^2) + 1813.5$, $r^2 = 0.87$. $PNUE_{SP} = 4.78 \times 10^{-3} (x) - 6.85 \times 10^{-7} (x^2) + 7.06$, $r^2 = 0.87$; $PNUE_{LS} = 6.87 \times 10^{-2} (x) - 1.14 \times 10^{-4} (x^2) - 6.23$, $r^2 = 0.85$. $RG_{RSP} = 4.07 \times 10^{-1} (x) - 3.31 \times 10^{-3} (x^2) + 53.99$, $r^2 = 0.89$; $RG_{RLS} = 8.28 \times 10^{-2} (x) - 3.76 \times 10^{-4} (x^2) + 39.59$, $r^2 = 0.97$.

content were related in a positive manner through direct effects on SLA, the mass of leaf relative to the mass of the entire plant (e.g., LWR), and the balance between respiration and photosynthesis (NAR). While N appears to be ample for sustained

growth in orchardgrass at each microsite, inadequate energy especially in young, newly established plants suggests that initial harvest should be deferred for SP plants at all sites, or LS plants growing at W. Photosynthetic capacity of leaves

depends on N concentration, which represents adaptation to light-restricted environments by increased N allocation to light capture mechanisms (Evans and Poorter 2001).

Photosynthetic nitrogen use efficiency

The PNUE declined as light attenuation increased and was less for SP than LS plants (Figure 1d). The PNUE of plants growing at W compared to O was 35% (SP) and 52% (LS) less. Plant PNUE decreased as RG_{RR} increased (Figure 4) and was less for SP than LS plants. Late-summer established plants at O, E_O and E_W have a relatively high DM production capability as a function of leaf N, relative to LS plants at W or SP plants at any site. Leaf N was inversely associated with PNUE (Figure 1c, d) and agrees with relationships of productivity expressed as a function of N and N concentration (see Freijsen and Veen 1989). The data also support the inverse relationship between light- and N-use efficiency presented by Hirose and Bazzaz (1998) and the relative N-enrichment of shaded environments (Wilson 1996).

Regardless of how growth indices are related, SP and LS plants behave as separate populations (representing young and established plants, respectively) with different leaf DM production

efficiencies. In SP and LS plants, PNUE relative to stembase TNC was least for plants at W, where stembase TNC was the least among microsites, regardless of planting time (Figure 3c). Stembase TNC was inversely related to RG_{RR} , with RG_{RR} greatest and TNC the least at W (Figure 3d). The relationship for RG_{RR} and TNC for SP plants growing at O and LS plants growing at W was similar. This reinforces observations that LS plants growing at W respond in a manner similar to SP plants and may require management practices suited to establishing or immature plants.

The observation that RG_{RR} differed among microsites despite morphological and physiological buffers (Meziane and Shipley 1999) might be a product of the defoliation regimen imposed in these experiments. Differences occurred although plants established in LS and growing at the W site had morphological and physiological indices of growth similar to SP plants growing under adequate light conditions.

Increased DM allocation to stembases in a competitive environment (*i.e.*, insufficient light because of canopy-related competition) enables plants to survive unfavorable conditions or regrow rapidly once the competition is relieved, by defoliation as an example (Chapin et al. 1990). The pattern of allocation to leaves suggests that micro-evolutionary response to competitive or selective pressures occur at a site. Orchardgrass can sustain leaf production when subjected to simultaneous stresses of shade and repeated defoliation. Defoliation often leads to high relative regrowth rates (Oosterheld and McNaughton 1991), since the influences of increased size and self-shading, as phytochrome-related changes occur are removed.

Planting orchardgrass in spring and clipping when an arbitrary canopy height is reached may impair sustained productivity of the plant in terms of accumulated TNC and restricted allocation to root and stembase mass (Belesky 2000). Management and environment interact along with planting time as N accumulates and TNC decreases with increasing light attenuation. This influences plant growth and forage nutritive value in terms of fermentable energy (TNC):protein quotient (Hoover and Stokes 1990). The different responses observed for SP and LS plantings might be related to chronological or physiological maturity of orchardgrass plants and warrants further investigation.

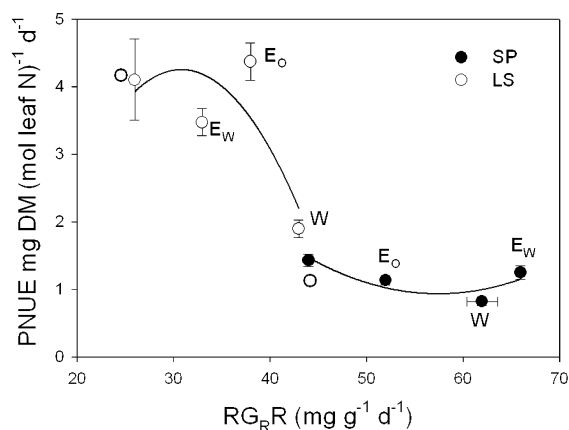


Figure 4. Photosynthetic N-use efficiency (PNUE) expressed as a function of relative regrowth rate (RG_{RR}) for plants established in spring (SP) and late-summer (LS) in the central Appalachian region of the eastern USA. Regression equations: $PNUE_{SP} = -3.44 \times 10^{-1} (x) + 2.99 \times 10^{-3} (x^2) + 10.80$, $r^2 = 0.73$; $PNUE_{LS} = 8.56 \times 10^{-1} (x) - 1.39 \times 10^{-2} (x^2) - 8.96$, $r^2 = 0.64$.

Acknowledgements

Joyce M. Ruckle, Biologist, provided untiring professional support with experiment procedure and data analysis. M.L. Huffman provided technical assistance. D.M. Burner and G.P. Cheplick commented on early drafts of the manuscript. Trade names are used for the convenience of the reader and do not imply endorsement by USDA over comparable products or services.

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